Juvenile growth and crown morphological plasticity of eastern white pines (*Pinus strobus* L.) planted along a natural light gradient: Results after six years

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Underplanting white pine (*Pinus strobus* L.) is a promising method to reduce competition and protect against white pine weevil (*Pissodes strobi* (Peck)) damage. However, shading caused by overstory trees can reduce growth, vigor and survival of white pine. The objective of this study was to determine the effects of a light gradient on the growth and overall crown morphology of white pine saplings planted in 3-meter strips within a hardwood forest some six years earlier. In 1994, we measured total height and diameter, leader length (in 1994) and numerous crown morphological variables. We then estimated the light environment above the crown of 63 young white pine saplings representing six families of close provenance. White pine grew well (i.e., >20 cm in height/year) for the first six years when planted at light levels between 10 and 66% of full sunlight. Total height and diameter after six years tended to decline more sharply below 30% full sunlight, confirming earlier experiments made in controlled conditions. No significant changes in crown morphology were evident along the light gradient. This lack of crown morphological plasticity presumably contributes to limiting the ability of white pine to grow and compete in a very low light environment. Various silvicultural options are discussed in light of the results obtained in this study.

Key words: Understory growth, white pine, understory planting, crown morphology, silvicultural options, light gradient

La plantation en sous-étage de pin blanc (*Pinus strobus* L.) constitue une méthode prometteuse de réduction de la compétition et de protection contre les dégâts du charançon du pin blanc (*Pissodes strobi* (Peck)). Toutefois, l'ombrage occasionné par les arbres des étages supérieurs réduit la croissance, la vigueur et la survie du pin blanc. L'objectif de cette étude visait à déterminer les effets d'un gradient de lumière sur la croissance et la morphologie générale de la cime de gaules de pin blanc plantées le long de bande de 3 mètres de largeur sous une forêt de feuillus quelque six ans auparavant. En 1994, nous avons mesuré la hauteur totale et le diamètre, la longueur de la pousse annuelle (de 1994) et plusieurs autres variables morphologiques. Nous avons par la suite estimé l'environnement lumineux au-dessus de la cime de 63 jeunes gaules de pin blanc issues de six familles de parenté rapprochée. Les pins blancs ont connu une bonne croissance (par ex., > 20 cm de hauteur/an) pour les six premières années pour les plants situés sous des niveaux d'ensoleillement entre 10 et 66 % du plein ensoleillement. La hauteur total et le diamètre après six ans avaient tendances à décliner plus radicalement lorsque l'ensoleillement était sous les 30 % de pleine luminosité, ce qui confirmait le résultat d'essais précédents réalisés sous des conditions contrôlées. Aucun changement significatif n'est apparu dans la morphologie de la cime en fonction du gradient d'ensoleillement. Ce manque de plasticité au niveau de la morphologie de la cime contribue vraisemblablement à la capacité du pin blanc de croître et de survivre dans un environnement de très faible luminosité. Différentes options sylvicoles sont abordées en fonction des résultats obtenus dans cette étude.

Mots-clés: croissance en sous-étage, pin blanc, plantation en sous-étage, morphologie de la cime, options sylvicoles, gradient d'ensoleillement

Introduction

Intensive harvesting of eastern white pine (*Pinus strobus* L.) for over a century has seriously reduced abundance in its entire range, and even resulted in localized extinction. Concerned about future supplies of timber, forest managers have promoted the use of reforestation with pure white pine plantations. However, such plantations have been shown to be very vulnerable to attack from white pine weevil (*Pissodes strobi* (Peck)), especially when grown under full or near full sunlight conditions (MacAloney 1930). One of the recently proposed silvicultural solutions is to plant white pine under the cover of shade intolerant hardwoods, thereby reducing light and heat levels to impede the growth and development of white pine weevil (Sullivan 1961, Stiell 1979, Berry 1982, Wallace and Sullivan 1985, Katovich and Morse 1992).

White pine is a mid-tolerant species that can regenerate itself and grow in understory gaps to achieve canopy recruitment (Wendell and Smith 1990, Peterson and Squiers 1995). Low light levels associated with shaded conditions may limit height and diameter growth (Bormann 1965, Logan 1966, O'Connell and Kelty 1994). Such growth reduction is usually accompanied by morphological changes at the crown level (O'Connell and Kelty 1994). These authors showed that white pine growing under a fully closed canopy slightly modified its height over lateral growth ratio, but these changes were less evident than those seen among true shade-tolerant conifers.

One might expect that the success of underplanted white pines will depend on the amount of light that reaches the understory. According to Logan (1966), approximately 45% of full sunlight is sufficient to reach maximum height growth in white pine. However, these results reflect controlled conditions where only light quantity was varied. O'Connell and Kelty (1994) measured growth and morphological acclimation of naturally regenerated white pine, but limited their comparison to a deeply shaded environment (5–15% full sunlight) and completely open conditions (100% full sunlight). The objective of the present study was to quantify effects after six years of a light gradient varying between 10 and 66% of full sunlight, caused by an overstory of intolerant hardwoods subjected to

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partial harvesting, on the juvenile growth and crown morphology of white pine planted in cut-strips.

Methods

Study Area

White pine saplings were selected in a provenance progeny test (Beaulieu *et al.* 1996, Li *et al.* 1996) located from an area approximately 60km northwest of Trois-Rivières, Québec, Canada (45°56′N, 70°29′W: Altitude = 150 m). Mean winter and summer temperatures were –10.6°C and 16.6°C, respectively, with an average of 102 frost-free days. Total annual precipitation averages 1041 mm; 259 mm falling as snow and 782 mm as rain (Environment Canada 1996). The study site is dominated by sandy humo-ferric podzols of fluvio-deltic origin.

White pine seedlings had been raised for one year in a greenhouse at the Laurentian Forestry Centre and then transplanted in a nursery located at the Valcartier Forest Experiment Station. In the spring of 1988, the four-year-old seedlings were planted in a second growth forest dominated by both trembling aspen (*Populus tremuloides* Michx.) and red maple (*Acer rubrum* L.) with an average canopy height of 18m. A young, dense understory stratum was also present, composed primarily of regenerating aspen and hardwood shrubs such as beaked hazel (*Corylus cornuta* Marsh.), speckled alder (*Alnus rugosa* (Du Roi) Spreng.), and mountain holly (*Nemopanthus mucronatus* (L.) Trel.).

Basal area before thinning (stems > 5 cm dbh) was estimated to be approximately $32m^2$/ha. Thinning by removing 3 m strips and leaving 5m bands between the cut-strips removed approximately half of the basal area. Several thousand eastern white pine saplings representing open-pollinated families originating from many geographically distinct provenances were planted in the 3m-wide strips. Following establishment in 1988, the plantation underwent several silvicultural operations including the application of a browsing repellent in August 1988, 89 and 90, as well as clearing around the pine saplings in May 1990.

Sample Sapling Selection

During the summer of 1994, 63 white pine saplings from six different half-sib families were chosen from the plantation layout with the objective of sampling a wide range of light levels. To minimize any possible provenance effect, we selected six families originating between 44.5° and 47.5°N from the province of Quebec to include enough saplings from a light gradient as wide as possible. We did not investigate provenance effect since a preliminary study by Li *et al.* (1996) showed that light availability had a similar effect on all white pine families. None of the sampled saplings showed any sign of weevil damage, and all possessed a straight, healthy crown. Only individuals from areas undisturbed (ignoring the clearing treatment) since plantation establishment were chosen to ensure that the light environment had not changed drastically in the ensuing six years. The dominant change in the light environment was due to the overstory forest canopy of trembling aspen and red maple, although some effects on lower branches due to hardwood shrub competition were unavoidable.

Characterizing the Light Environment

The percentage of above-canopy light (percent of photosynthetic photon flux density (400 to 700 nm), hereafter called % PPFD) reaching the top of each sapling crown was used to characterize the light environment of each individual. Light measurements were taken under completely overcast sky conditions following the method proposed by Messier and Puttonen (1995) and Parent and Messier (1996). These studies have shown that instantaneous measurements obtained under completely overcast sky conditions are a good estimate of the mean daily percent PPFD under both overcast and clear sky conditions. On completely overcast days (solar disk not visible), instantaneous light measurements using a Li-189 quantum sensor (LI-COR, Lincoln, NE, USA) were taken just above the terminal leader (I_u). Another quantum sensor linked to a LI-1000 datalogger (LI-COR) was placed in an adjacent clear-cut to record full overstory %PPFD conditions (I_o). The I_u value obtained at a certain time was divided by I_o recorded at the same time to calculate the above canopy %PPFD (%PPFD) transmitted above each leader.

Morphological And Growth Parameters

For each sapling, we measured total height (H), terminal leader length (Tl), length of the longest lateral branch of the first whorl (Br), live crown length (Cl), average crown diameter (Cd) and root collar diameter (Rd). Morphological plasticity of the crown was described using three ratios: 1) Cl:Cd, 2) Cl:H, and 3) Tl:Br.

Data Analysis

Linear regression models (Systat 1992) were used to describe growth and crown morphology variation along the light gradient. When necessary, data were transformed using natural logarithms to make the relationships linear or to respect assumptions of the regression models.

Results and Discussion

Height and Diameter Growth

The %PPFD in the understory estimated above the terminal leaders ranged from 10% to 66% of that received above the canopy. Within this range, decreases in %PPFD resulted in significant decreases in total height and diameter of juvenile white pines (Fig. 1A and B). This decrease was particularly evident below approximately 30% PPFD, especially if we removed one possible outlier at around 10% PPFD. The figures also suggest that both total height and diameter somewhat plateaued above 40% full sunlight, confirming earlier experiments made in controlled conditions (Logan 1966). Leader length was only marginally affected by % PPFD ($R^2 = 0.15$, P=0.11). Most white pine grew on average more than 20 cm in height per year. This is similar to rates reported by Kelty and Entcheva (1993) for understory pines following a heavy shelterwood cut. They reported that heavily suppressed white pine grew less than 10 cm per year. This seems to suggest that our six-year-old planted saplings were not heavily suppressed by the light gradient found in the understory. Similar effects of a light gradient on growth *in situ* have been reported for more shade-tolerant conifers (Klinka *et al.* 1992, Parent and Messier 1995, Chen *et al.* 1996). However, shade-tolerant conifers tended to reach maximum growth at lower light levels of approximately 25% PPFD and to have a much reduced height growth at low light levels.

Crown Morphology

None of the three crown morphology indices measured (Cl:Cd, Cl:H, and Tl:Br) or the ratio of height over root collar diam-

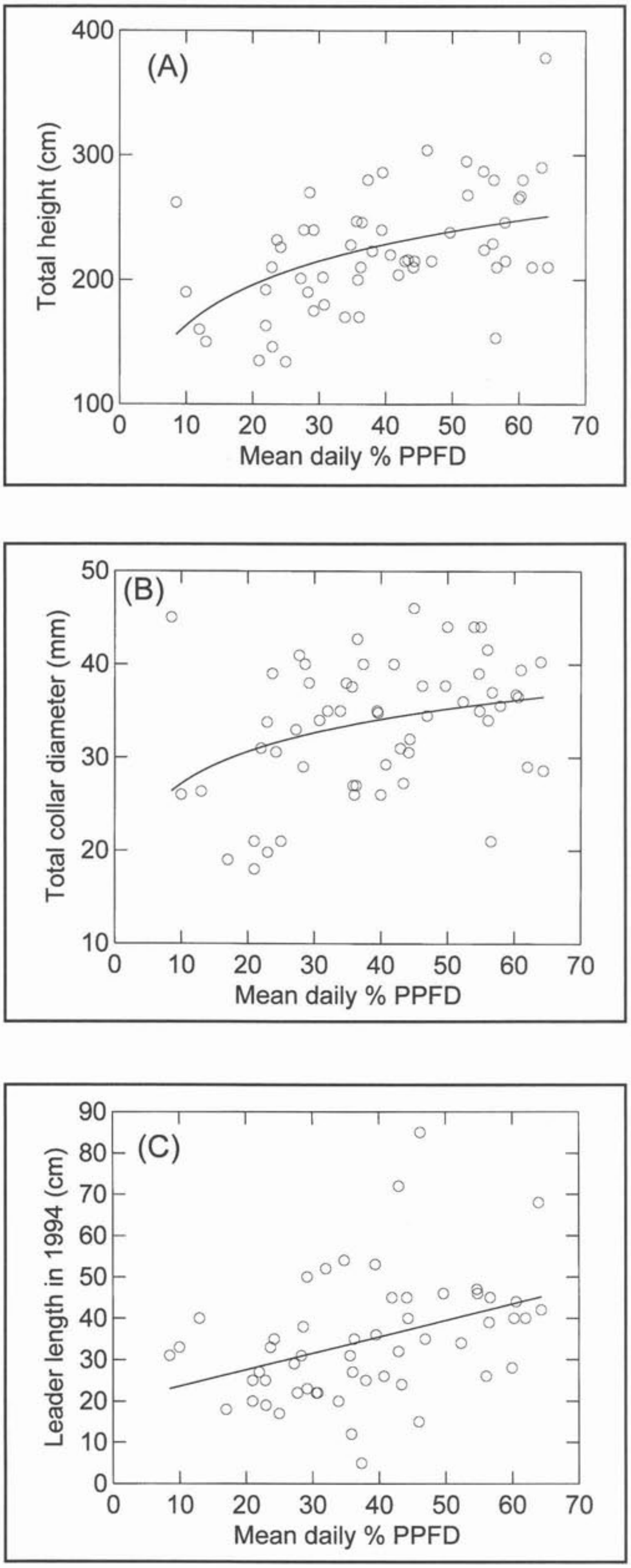

Fig. 1. Effects of increasing %PPFD above the terminal leader on (A) total height (cm) after six years (Ln (Height)= 0.26 x ln (%PPFD)+4.48; $R^2 = 0.291$, $P< 0.001$), (B) total diameter (mm) at root collar after six years (Ln (Diam)= 0.3 x Ln (%PPFD) + 2.38; $R^2 = 0.290$, $P= 0.002$) and (C) height increment (cm) of leader in 1994 (relationship is not significant: $R^2= 0.15$, $P=0.11$) of juvenile eastern white pines.

eter (H:Rd) were significantly correlated with light availability (Fig. 2.). O'Connell and Kelty (1994) described small but significant differences in several crown morphological parameters between natural white pines growing under a closed canopy (5–15% PPFD) and those growing in open conditions (*i.e.*, full sun, 100% PPFD). Our results are based on data collected between these two extremes (i.e. 10 to 66% PPFD), and average results fall between these two extremes. Among shade-tolerant conifers, the three crown morphological parameters (Cl:Cd, Cl:H and Tl:Br) usually decline with a reduction in light (Kohyama 1980, O'Connell and Kelty 1994, Parent and Messier 1995). Our pine saplings did not show such a decline as reported for shade-tolerant conifers at low light levels. Generally, Tl:Br was >1 and the live crown comprised greater than 90% of the total height in all light conditions (Fig. 2.). White pine appears to modify its crown morphology slightly only when light levels reach values lower than 10% PPFD (O'Connell and Kelty 1994).

Conclusion and Silvicultural Implications

Our results suggest that it is possible to grow planted white pines in the understory of an intolerant hardwood canopy for the first six years when there is at least 10% PPFD reaching the understory. However, both total height and diameter tended to be maximal at %PPFD greater than 40%, confirming earlier experiments made in controlled conditions by Logan (1966). These results tend to confirm that white pine is a mid-tolerant species that can grow well in understory gaps. Recent studies (Waring 1987, Givnish 1988, Gerrish 1990, Messier 1996, Messier *et al.* 1998) all suggest that tree light requirement increases with size, so that understory white pines would presumably require more light as they grow in size. The degree to which increasing size affects minimum light requirements is not yet known for white pine, but it is likely that a low intensity thinning would not be enough for white pine to reach overstory canopy dominance. Several silvicultural options exist, however. A low intensity thinning that allows at least 10% PPFD could allow a satisfactory growth of understory white pine for several years, as shown in this study, while inhibiting the growth of several less tolerant common understory woody shrubs such as raspberry for example (Ricard and Messier 1996). Such low intensity thinning could then be followed by another more intensive thinning to allow the white pine to reach overstory status. Alternatively, a higher intensity thinning that allows between 30 and 40% PPFD followed by some understory brushing a few years following the treatment, as was done in this study, would maximize white pine understory growth for many years, and could be sufficient for white pine to reach overstory canopy dominance without any other treatment.

The inability of understory white pine to grow and survive in deep shade is presumably the outcome of complex physiological and morphological interactions between leaf- and plant-level responses to light, nutrient and water availability (Givnish 1988, 1995; Messier *et al.* 1998). White pine tends to show little physiological plasticity in relation to light (Wetzel and Burgess 1994). In this paper, as well as in that of O'Connell and Kelty (1994), we suggest that this inability of white pine to grow and survive in deep shade is also related to its lack of crown morphological plasticity in relation to changes in light availability.

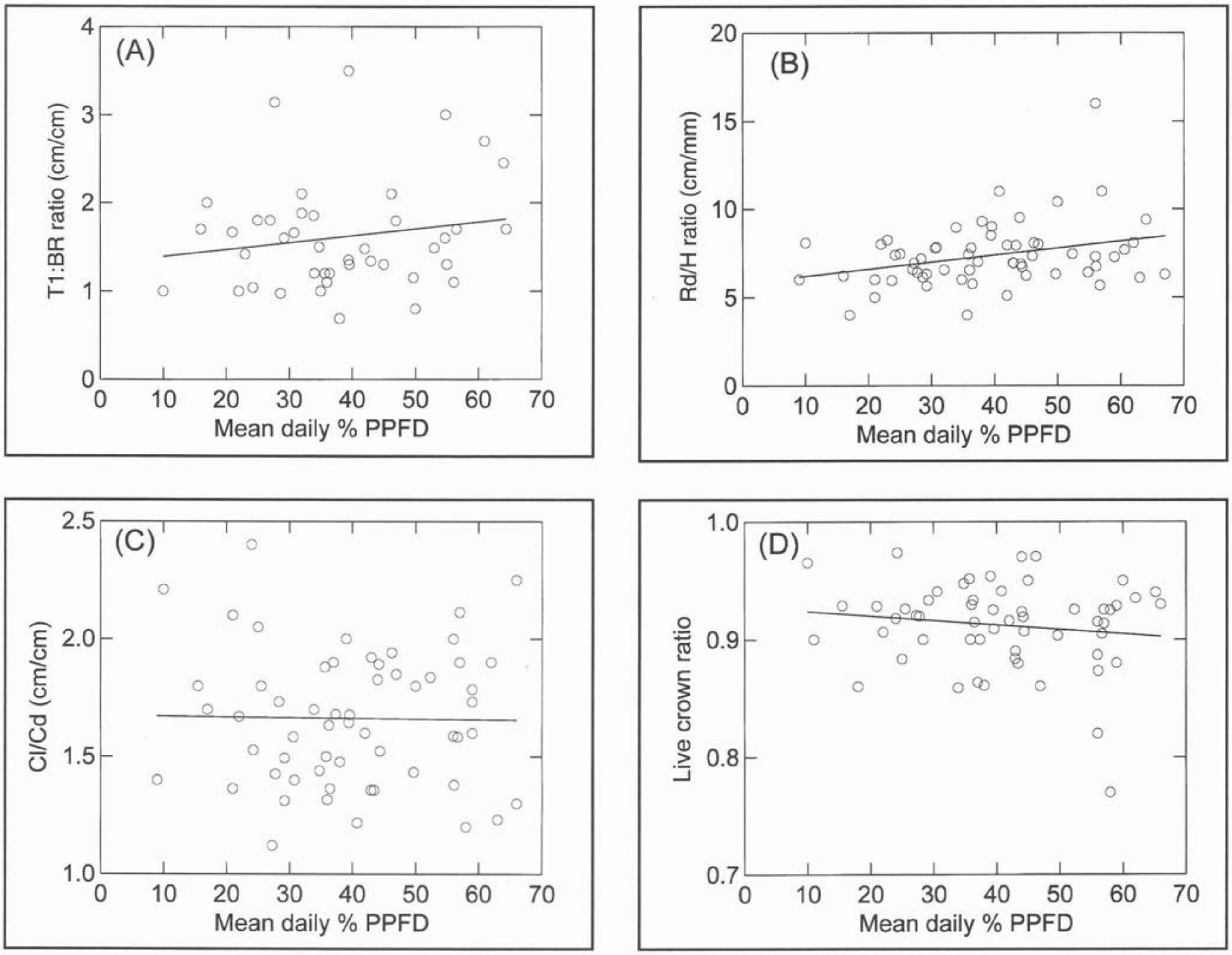

Fig. 2. Effects of increasing %PPFD above the terminal leader on (A) Tl:Br (ratio of terminal leader length over length of the longest lateral branch of the first whorl), on (B) Rd:H (ratio root collar diameter over height), on (C) C1:Cd (ratio of crown length over crown width, and on (D) on Cl:H (Live crown length over total height (live crown ratio). None of these relationships were significant with R^2 varying between 0.02 to 0.10 and P values varying between 0.23 to 0.89.

Future studies should attempt to quantify the %PPFD which is sufficient to allow white pine to reach overstory canopy dominance, yet minimize losses due to white pine weevil attack. Some preliminary results indicate that over the entire plantation of several thousands pines, light levels varied from 2–100% full sunlight and white pine lost to weevil approached 0.6% five years after plantation establishment (Li *et al.* 1996).

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